

Resistance among Populations of Yellow Starthistle to Thistle-Head Insects: Results from Garden Plots in Italy

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Variation in resistance to thistle-head insects was studied in plants of *Centaurea solstitialis* L. (yellow starthistle) derived from Nearctic and Palearctic populations and grown in common gardens near Rome, Italy. Significant variation was found in the percentage of insect-damaged flowerheads among plant populations, with aggregate rates of herbivory higher on plants of the local (Italian) population. Two tephritid flies, *Acanthiophilus helianthi* (Rossi) and *Chaetorellia succinia* (Costa), accounted for most of the damage to all populations. In addition, more species of insects exploited the capitula of Italian plants (eight vs three to six species for the other populations). That only Italian plants were suitable host plants for *Urophora jaculata* Rondani suggests a host-plant resistance factor was responsible for the failure of this tephritid fly to become established on yellow starthistle in California. These results indicate that all populations of yellow starthistle are not equally susceptible to herbivory by thistle-head insects. On the other hand, adults of two potential biocontrol agents, *U. quadrifasciata quadrifasciata* (Meigen) and *Terellia uncinata* White, emerged from American plants; thus, there is reason to believe these tephritid flies would establish on Nearctic populations. Variation in resistance among plant populations was not related to differences in plant size. The overall results are consistent with the findings of other ecologists that noncrop plant species vary significantly in their resistance to individual herbivore species and to groups of insect herbivores. The results also point to the usefulness of the open field approach in host-specificity determination of insects for biological control of weeds.

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INTRODUCTION

The ubiquity of genetic variation in crop plants and their wild relatives provides plant scientists with the

means to develop pest-resistant crop cultivars. On the other hand, genetic variation among populations of weedy plants might hamper the efforts of practitioners of biological weed control to use insects and pathogens as biocontrol agents against adventive forms of these plants. For example, underlying genetic variation among Palearctic and Nearctic populations of yellow starthistle (*Centaurea solstitialis* L.) is thought to have led to the failure of *Urophora jaculata* Rondani (Diptera: Tephritidae) [misnamed *U. sirunaseva* (Hering) (see White and Clement, 1987)] to establish on populations of the weed in California (Ehler and Andres, 1983). This fly was imported from Italy, where it readily attacked and completed its development in the capitula of yellow starthistle. As a result of this and other unsuccessful attempts to establish potential biocontrol agents on naturalized weeds, Ehler and Andres (1983) suggested that "host incompatibility has been a major factor in the failure of exotic, host-specific, weed-feeding arthropods to become established" on populations of target weeds in North America.

Yellow starthistle is an introduced, widespread annual weed in the United States. Weed biocontrol workers are attempting to control this weed with host-specific, insect natural enemies from the plant's native regions in southern Europe and Turkey (Clement, 1990; Turner *et al.*, 1993). In response to the failure of *U. jaculata* to become established on yellow starthistle in California in the 1960s and 1970s, USDA-ARS weed biocontrol workers in Italy and Greece began incorporating plants derived from Nearctic populations of the target weed into laboratory and open-field host-specificity tests for new biocontrol agents in the 1980s (Clement *et al.*, 1988; Clement *et al.*, 1989; Clement and Sobhian, 1991).

This study was designed to measure variation in susceptibility to thistle-head insects among Nearctic and Palearctic populations of yellow starthistle under uniform field conditions in central Italy. Herein I present data on the exploitation of these different plant populations by a suite of thistle-head insects and by members

of this guild that may have potential as biocontrol agents for use against yellow starthistle. Such information is important because resistance among Nearctic populations to insect herbivory could prevent the establishment of new biocontrol agents in the United States. This paper also addresses the possible influence of selected plant attributes (phenology of bud and flower formation and plant size) on the intensity of insect herbivory. Some of the data generated in this study on *Urophora* (Diptera: Tephritidae) host utilization patterns were presented in an earlier report on *Urophora* fly systematics and host-plant associations by White and Clement (1987).

MATERIALS AND METHODS

Plot Establishment and Design

Experimental gardens were established in 1984 and 1985 in the same plot space (12×12 m) on the grounds of the USDA-ARS Biological Control of Weeds Laboratory in Rome, Italy. The 1984 garden contained plants of two Palearctic [Rome, Italy (control); southern Spain] and five Nearctic (Walla Walla, Washington; Yakima, Washington; Lapwai, Idaho; Sacramento, California; Contra Costa County, California) populations of yellow starthistle and a cultivar ("Hartman") of safflower (*Carthamus tinctorius* L.) arranged in an 8×8 Latin square (64 plots). In 1985, plants of three Palearctic (Rome; southern Spain; Thermi, Greece) and two Nearctic (Lapwai, Idaho; Sacramento, California) populations of yellow starthistle and the cultivar of safflower were arranged in a randomized block design with four replications (24 plots). Rows were designated in a north-south direction in each garden.

The cultivated safflower, a crop plant taxonomically related to yellow starthistle, was included to ascertain its suitability as a host plant for potential biocontrol agents. However, meaningful data on this aspect of host specificity were not collected during this study because of phenological asynchrony between the safflower and yellow starthistle plants.

Rosettes of yellow starthistle were grown from seed in a glasshouse and transplanted into plots between 3 and 5 April 1984 and 1985. This period coincides with the natural occurrence of rosettes in central Italy (Clement *et al.*, 1989). When transplanted, rosettes were 8 to 12 cm in diameter with 8 to 10 basal leaves [early rosette phase according to Maddox (1981)]. One rosette was placed in the center of each 1.5×1.5 -m plot. The plots were adjacent to each other and areas between plots were weeded by hand or machine-tilled to remove unwanted plants. Occasional rain was the only source of water after newly transplanted plants were watered by hand.

Insect Herbivory

All yellow starthistle capitula in the anthesis stage (F2 in Clement, 1990) from each plant were collected at 5- to 14-day intervals between 15 July and 2 October 1984 and every 7 days between 2 July and 3 September 1985. Predacious spiders on outer surfaces of capitula were removed before samples were placed in 500-ml cardboard cartons capped with nylon organdy to retain emerging insects. There were one to three cartons per plant sample per collection date. Cartons were placed on a table in a laboratory (15–32°C; natural lighting) and were checked one to three times a week until samples were dissected. Emerging insects were pinned and later identified with the aid of a voucher collection of thistle-head insects at the USDA-ARS Laboratory in Rome, Italy, and with the help of taxonomic specialists. Emerging parasitoids were not always counted and none were identified.

In March and April 1985 and 1986, all capitula >5 mm in diameter ($n = 36,645$) were dissected and carefully examined for the presence of immature and adult insects, or evidence that larvae had previously fed in the capitula. Small capitula (<5 mm) were not dissected because previous work showed that these rarely harbored insects (S. L. Clement, unpublished information). The numbers of adult insects found in dissected samples were combined with the numbers of previously emerged adults to estimate the total emergence of each insect species per yellow starthistle population.

The presence of the receptacle galls of *U. jaculata* in flowerheads was recorded to determine the ability of individual host populations to support infestations of this fly. Information of this type was not generated for any other species, in large part because I was unable to differentiate all dead and parasitized larvae of ovule- and achene-feeding insects (e.g., *Acanthiophilus helianthi* (Rossi) and *Chaetorellia succinia* (Costa) (Diptera: Tephritidae)). Therefore, I calculated an aggregate rate of insect-damaged capitula for each plant population.

Data from monthly samples were grouped because too few samples were collected on some sample dates to permit meaningful comparisons of insect infestation rates. In two instances (Sept. + Oct. 1984; Aug. + Sept. 1985) it was necessary to group data from 2 months. Data (percentages of insect-damaged capitula per plant per population group) were transformed using the arcsine transformation and analyzed with a two-way ANOVA model (population by block) (SAS-GLM; SAS Institute, 1987) to determine whether plants from different populations differed in susceptibility to thistle-head insects. The sample variance ratio procedure and the F_{\max} test (Sokal and Rohlf, 1981) were used to ensure that the assumption of homogeneity of variances was met before the transformed data were analyzed. Dun-

can's multiple range test was used to determine differences among all means. Untransformed means are reported herein.

Throughout this study I carefully examined plants for ectophagous insect herbivores. None was found in 1985. In 1984, however, small numbers of larvae of a small moth (wing span about 7 mm), *Tebenna* sp. prob. *micalis* (Mann) (Lepidoptera: Choreutidae), were found feeding on the leaves and stems of 11 plants in the rosette and bolting stages. The growth and development of these plants were seemingly unaffected by the presence of this insect (S. L. Clement, unpublished information).

Plant Phenology and Appearance

In 1984, data on flowerhead collections (F2 stage in Clement, 1990) from each population were cast into cumulative frequency distributions. In 1985, collections of late-stage, closed capitula (B4 stage in Clement, 1990) were cast into cumulative frequency distributions because it was apparent in 1984 that closed buds were the oviposition substrates of most of the species within the local assemblage of thistle-head insects. This was accomplished by tagging three branches (one each on the lower, middle, and upper portions of a plant) on each of three randomly selected plants per population and totaling the number of B4 buds on these branches every 7 days between 4 June and 19 August. The Kolmogorov-Smirnov two-sample test ($P = 0.05$) ($n < 25$; Sohal and Rohlf, 1981) was used to determine whether the distribution of flowering (1984) and bud formation (1985) over time (phenology) differed between plant populations.

The height and width of each plant were measured in mid-August 1984 and 1985, after growth had ceased. The mean height and width of mature plants of different populations were compared using two-way ANOVA and Duncan's multiple range test (GLM-SAS; SAS Institute, 1987). Data were transformed ($\log x$) before analyses; however, untransformed means are reported.

Because plant size varied in a 1983 garden plot study in Rome, Italy (S. L. Clement, unpublished information) and in this study (see Results and Discussion for measures among populations), I hypothesized that such heterogeneity could influence levels of insect herbivory. For example, did larger, more apparent plants suffer more from herbivory? Herein, plant height and width were correlated (Pearson correlation coefficients; SAS Institute, 1987) separately with the proportion of insect-damaged capitula at two levels: at the individual plant level and at the plant population level.

RESULTS AND DISCUSSION

Insect Herbivory

Eleven species of insects were reared from the capitula of yellow starthistle, eight of which exploited the

capitula of Italian plants. Lower numbers of species (three to six) attacked the capitula of other plant populations. I attribute the higher number of insect species associated with Italian plants to the fact that *U. jaculata* and *Isocolus* sp. (Hymenoptera: Cynipidae) only attacked the local population (Table 1). Receptacle galls of *U. jaculata* were found only in samples from Italian plants (18 galls in 1984 and 16 galls in 1985 samples).

In both years, all plant populations were not equally suitable as hosts to the complex of thistle-head insects that colonized the garden plots. These observed patterns were due to treatment effects; block effects ($P > 0.05$) were not a factor (Tables 2 and 3). Tables 2 and 3 also summarize the seasonal course of insect herbivory for 1984 and 1985, respectively, and show that infestation levels were consistently higher ($P < 0.05$ except during the August–September 1985 sampling period) on Italian plants for which percentages of insect-damaged capitula averaged 31.4% in 1984 and 23.7% in 1985 [percentages compare favorably with levels of 14–37.9% reported by Clement and Mimmocchi (1988) for six populations on the central- and south-Italian mainland]. Indeed, even among Palearctic populations, herbivore loads were noticeably higher on plants of the Italian population. The two most common species (*A. helianthi* and *C. succinia*) (Table 1) undoubtedly accounted for most of the damage to capitula, and hence for the largest part of the variation in herbivore loads among plant populations.

Potential biocontrol agents. Three potential biocontrol agents, namely the cynipid wasp *Isocolus* sp. and the tephritid flies *Terellia uncinata* White and *Urophora quadrifasciata quadrifasciata* (Meigen) (Clement, 1990) were among the 11 species of insects that colonized the plots. As only three specimens of *Isocolus* were recovered, all from Italian plants, no definite conclusions can be made about the ability of this wasp to attack American plants. Because the taxonomy of the genus *Isocolus* is unclear (Sobhian and Zwölfer, 1985), it is not certain whether the wasps that emerged from Italian plants are the same species as the ones that emerged from the capitula of American plants of yellow starthistle in a 1985 garden plot in Greece (Clement and Sobhian, 1991). Likewise, only three adults of *T. uncinata* were recovered; however, two emerged from plants derived from the Nearctic populations. Thus, there is reason to believe this fly would establish itself on American plants. This study revealed no overt resistance in yellow starthistle to *U. q. quadrifasciata* as several adults of this potential biocontrol agent emerged from American and European plants (Table 1). Interestingly, *U. q. quadrifasciata* occurs in Canada and parts of the western United States, where it attacks spotted knapweed (*Centaurea maculosa* Lam.) and diffuse knapweed (*C. diffusa* Lam.) but not yellow starthistle (White and Clement, 1987).

TABLE 1

Taxonomic Composition and Number of Insects Reared from Capitula of Plants of Palearctic and Nearctic Populations of Yellow Starthistle Grown Together in Garden Plots, Rome, Italy, 1984 and 1985

Insect species	No. emerging insects/host plant population/year ^a													
	IT		SP		GR	ID		CA-S		CA-C	WA-W	WA-Y	Total	
	1984	1985	1984	1985	1985	1984	1985	1984	1985	1984	1985	1984	1984	1985
Diptera														
Tephritidae														
<i>Acanthiophilus helianthi</i> (Rossi)	107	10	1	46	2	24	28	24	2	49	46	20	271	88
<i>Chaetorellia succinia</i> (Costa)	41	130	11	64	28	37	50	118	49	40	138	94	479	321
<i>Terellia uncinata</i> White	1	0	0	0	0	0	1	0	0	0	1	0	2	1
<i>Urophora jaculata</i> Rondani ^b	3	6	0	0	0	0	0	0	0	0	0	0	3	6
<i>Urophora quadrifasciata</i>														
<i>quadrifasciata</i> (Meigen) ^b	2	38	0	2	2	2	17	2	2	2	1	0	9	61
Coleoptera														
Anobiidae														
<i>Lasioderma</i> sp. nr.														
<i>haemorrhoidale</i> (Illiger)	0	1	1	15	0	3	2	3	3	6	1	2	16	21
Lepidoptera ^c	1	0	1	0	2	0	1	0	0	1	1	0	4	3
Hymenoptera ^d	3	0	0	0	0	0	0	0	0	0	0	0	3	0
Total	158	185	14	127	34	66	99	147	56	98	188	116	787	501

^a IT, SP, GR, ID, CA-S, CA-C, WA-W, and WA-Y represent *C. solstitialis* plants grown from seed collected in Italy (Rome), southern Spain, Greece (Thermi), Idaho (Lapwai), California (Sacramento), California (Contra Costa County), Washington (Walla Walla), and Washington (Yakima), respectively.

^b Data previously presented in a paper on *Urophora* systematics (White and Clement, 1987) but is listed here for completeness.

^c Emerging Lepidoptera were *Pyroderces argyrogrammus* (Zeller) (Cosmopterigidae), CA-C and GR populations; *Metzneria* sp. (Gelechiidae), IT and SP; *Eublemma parva* (Hübner) (Noctuidae), ID and GR; and an unidentified species, WA-W.

^d Emerging Hymenoptera were *Isocolus* sp. (Cynipidae).

The fly population that exploited the experimental plantings of yellow starthistle in this study and the one that already occurs in North America may be different host races or separate biological species (White and Clement, 1987; White and Korneyev, 1989). This question cannot be resolved, however, without more study. Prior to this study it was not known that Nearctic populations of yellow starthistle would serve as suitable host plants for a Mediterranean population of the fly presently known as *U. q. quadrifasciata*.

That low numbers of *Isocolus*, *T. uncinata*, and *U. q. quadrifasciata* emerged from yellow starthistle does not by itself make these insects unpromising biocontrol agents. Other natural enemies of yellow starthistle [*Bangasternus orientalis* (Capiomont), *Larinus curtus* Hochhuth (Coleoptera: Curculionidae); *U. sirunaseva*] were recorded in low numbers in a garden plot study in southern Europe (Clement and Sobhian, 1991), yet evidence indicates their populations are on the increase in areas of the western United States where they have become established (S. L. Clement, unpublished information). It is likely that populations of insect natural enemies of yellow starthistle in southern Europe are maintained at low levels by parasitoids (Sobhian and

Zwölfer, 1985; Clement and Sobhian, 1991; S. L. Clement, unpublished information). When these natural enemies are introduced into the United States without their parasitoids they have the potential to attain high population densities.

Other species encountered in this study have been rejected for development as biocontrol agents, including *A. helianthi* and *C. succinia* (see Clement, 1990). *Acanthiophilus helianthi* attacks safflower and many other species in the tribe Cardueae (White *et al.*, 1990). Although *C. succinia* is specific to the genus *Centaurea*, it is very closely related to *C. carthami* Stackelberg, a pest of cultivated safflower (White and Marquardt, 1989); therefore, it was rejected as a potential agent for fear that it might adapt to attacking safflower (Sobhian and Zwölfer, 1985).

Plant Phenology and Appearance

No significant differences ($P > 0.05$) in flowering (1984) and bud (1985) phenology were detected when cumulative distributions of the population groups were compared (Kolmogorov-Smirnov two-sample test: D_{\max} values ranged from 0.111 to 0.333 and from 0.125 to

TABLE 2

Mean Percentages (\pm SEM) of Insect-Damaged Capitula from Plants of Seven Populations of Yellow Starthistle, Rome, Italy, 1984

Population ^a	Sampling period			
	July	Aug.	Sept. and Oct.	Entire season
Palaearctic				
IT	32.6 (5.3)a ^b	31.3 (3.9)a	32.9 (5.3)a	31.4 (3.9)a
SP	1.1 (0.7)c	4.1 (0.5)d	2.1 (1.1)b	3.2 (0.3)d
Nearctic				
ID	8.3 (1.2)b	11.4 (1.1)c	8.9 (2.9)b	10.5 (0.8)c
CA-S	6.4 (2.1)b	11.7 (1.8)c	6.8 (2.2)b	9.8 (1.6)c
CA-C	6.8 (1.8)b	12.7 (2.0)c	4.6 (2.1)b	10.1 (1.4)c
WA-W	11.1 (3.9)b	21.2 (3.7)b	4.6 (4.1)b	16.0 (1.2)b
WA-Y	10.9 (3.9)b	14.1 (1.8)c	7.5 (2.3)b	12.4 (1.7)bc
<i>F</i> values ^c				
Treatments	13.96***	15.29***	9.16***	24.47***
Blocks	1.40 NS	1.15 NS	0.92 NS	0.91 NS

^a Population codes are associated with specific populations in Table 1.

^b Means within columns followed by dissimilar letters are significantly different ($P = 0.05$) according to Duncan's multiple range test. Latin square design used but analysis of results done in accordance with randomized block design because one treatment (safflower) was deleted (see text).

^c NS, not significant.

*** $P < 0.001$.

0.278, respectively, for all comparisons in 1984 and 1985) (Fig. 1). Thus, phenological asynchrony was not a factor influencing the observed patterns of insect herbivory.

On the other hand, average plant sizes varied significantly among plant populations. In 1984, differences were significant ($P < 0.05$) for plant width and plant height, with the Italian, Spanish, and Yakima, Washington populations having the smallest (thinner and shorter) plants (Table 4). In 1985, Italian plants were significantly shorter ($P < 0.05$); they were also thinner than plants of other population groups, but differences were not statistically significant ($P > 0.05$) (Table 4). Plant width and height were significantly correlated ($r = 0.87$, $P < 0.05$) in 1984; however, these measures were not correlated ($r = 0.34$, $P > 0.05$) in 1985 when each population was represented by only four plants.

When mean values for plant height and width were correlated separately against proportions of insect-damaged capitula at the plant population level, the values of r ($P > 0.05$) were: height, 0.19 and width, 0.12 (1984); height, 0.57 and width, 0.48 (1985). Indeed, small Italian plants suffered significantly more damage ($P < 0.05$) than did similarly sized plants of the Spanish and Yakima, Washington populations in 1984 (Tables 2 and 4). In addition, some populations with large plants experi-

enced some of the lowest levels of herbivory (e.g., the two California populations in 1984) (Tables 2 and 4). Also, plant size and herbivore loads were uncorrelated ($P > 0.05$) at the individual plant level (data and r values not shown). Likewise, Moore (1978) and Bach (1981) reported no significant relationship between plant size and herbivore abundance. However, in other studies involving different plants and herbivore species, heterogeneity in plant size was related to differences in herbivore infestation levels (Solomon, 1981; Windig, 1993). In conclusion, other plant traits (physical and chemical) and mechanisms not measured or considered in this study no doubt contributed to the different infestation levels among plant populations.

Concluding Remarks

To the questions of whether or not yellow starthistle populations exhibit differences in susceptibility to thistle-head insects in general, and if such differences in host plant quality could affect the success of a biological control agent, the answer is "yes" on both accounts. That *U. jaculata* failed to establish itself on yellow starthistle in California is consistent with suggestions (Barrett, 1982; Schultz, 1991) that host-plant resistance in weedy plants targeted for biological control could adversely affect the success of biocontrol agents. On the other hand, this study provided no evidence that inter-population variation in host quality would prevent the establishment of potential biocontrol agents like *U. q.*

TABLE 3

Mean Percentages (\pm SEM) of Insect-Damaged Capitula from Plants of Five Populations of Yellow Starthistle, Rome, Italy, 1985

Population ^a	Sampling period		
	July	Aug. and Sept.	Entire season
Palaearctic			
IT	29.8 (6.0)a ^b	16.3 (2.4)a	23.7 (3.7)a
SP	11.6 (4.1)b	6.1 (2.0)a	10.0 (2.1)b
GR	7.7 (1.3)b	11.9 (1.2)a	8.4 (0.9)b
Nearctic			
ID	16.2 (2.0)b	14.1 (4.0)a	15.2 (2.2)b
CA-S	8.2 (1.1)b	12.6 (2.3)a	9.8 (1.6)b
<i>F</i> values ^c			
Treatments	8.21**	2.63 NS	6.94**
Blocks	1.47 NS	2.84 NS	0.77 NS

^a Population codes are associated with specific populations in Table 1.

^b Means within columns followed by dissimilar letters are significantly different ($P = 0.05$) according to Duncan's multiple range test.

^c NS, not significant.

** $P < 0.01$.

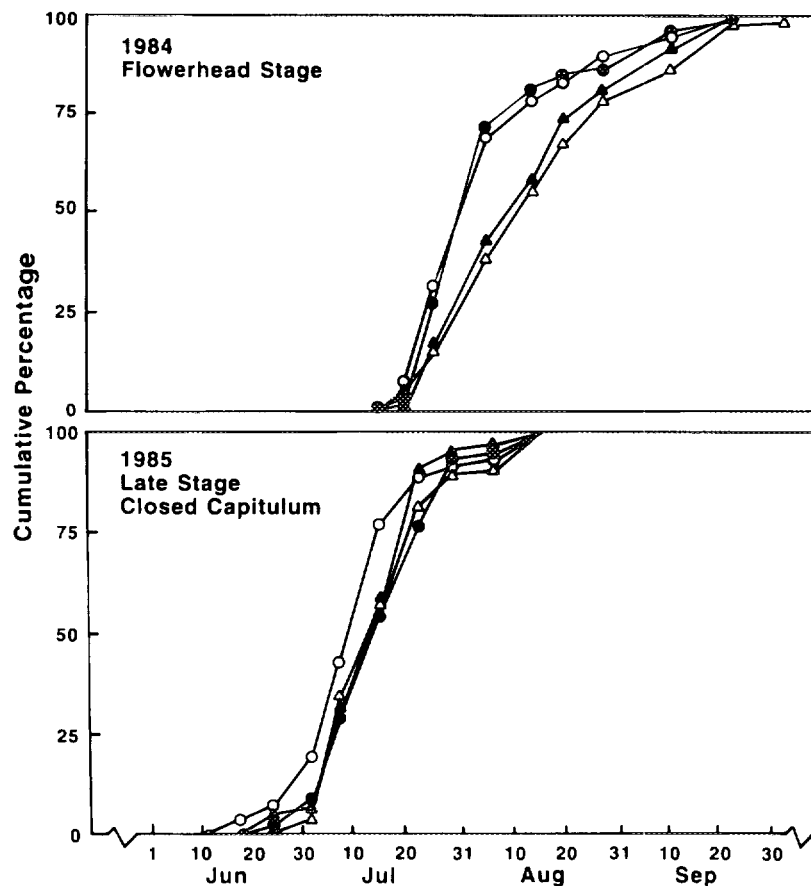


FIG. 1. Cumulative percentage of development of flowerheads (1984) and late stage buds (1985) on yellow starthistle from Italy (●), Spain (▲), Idaho (○), and Sacramento, California (△). Data depicted for only four populations to avoid presenting a cluttered view of several phenology curves. Phenology rate curves within a year are not significantly different (D_{\max} values less than critical values for all possible comparisons, $P = 0.05$; Kolmogorov-Smirnov two-sample test).

quadrifasciata and *T. uncinata* in the western United States.

While I do not know whether the lower aggregate infestation rates on Spanish, Greek, and American plants of yellow starthistle were due to antibiotic and/or anti-xenotic activity in these plants toward insect herbivory, there is good evidence that antibiosis was responsible for the resistance of some plant populations to *U. jaculata*. This was provided by D. M. Maddox (personal communication in Ehler and Andres, 1983) who observed that *U. jaculata* oviposit on yellow starthistle in California, with subsequent egg hatch but no significant larval development. The basis for the plant resistance observed in this study to both monophagous (hosts restricted to the genus *Centaurea*; e.g., *U. jaculata* and *C. succinia*) and polyphagous (hosts include several Cardueae species; e.g., *A. helianthi* and *Lasioderma* sp.) members of a guild of thistle-head insects is presumed to be genetic.

How genetic resistance in American yellow starthistle to *U. jaculata* arose is a matter of speculation. Is this an

example of a formerly coevolved pest-enemy system reunited after the pest had evolved free of its natural enemy for a considerable period of time (defined as a "quasi-old" association by Ehler, in press)? Yellow starthistle likely was introduced into California between 1824 and 1869 (Maddox, 1981); thus, it had over 100 years to undergo genetic change before insect biocontrol agents were introduced into the western United States (see Maddox *et al.*, 1986). Alternatively, the results could indicate that yellow starthistle in the United States originated outside of the geographical range of *U. jaculata* (Turner *et al.*, in press).

With increasing frequency, ecologists are discovering that individual plants, plant clones, and populations of noncrop species vary significantly in their susceptibility to individual species and to groups of insect herbivores (e.g., Hare, 1980; Maddox and Root, 1987, 1990; McCrea and Abrahamson, 1987; Moran and Whitham, 1990). The results of this study are testimony to the existence of insect resistance in a weedy thistle targeted for biological control. Finally, the results point to the usefulness

TABLE 4

Mean (\pm SEM) Width and Height (cm) of Mature Plants of Different Populations of Yellow Starthistle, Rome, Italy, 1984 and 1985

Population ^a	Plant width (cm)		Plant height (cm)	
	1984	1985	1984	1985
Palaearctic				
IT	93.0 (3.6)bc ^b	84.8 (13.8)a	75.4 (1.9)ab	62.8 (4.4)a
SP	80.3 (4.6)ab	112.3 (4.1)a	71.9 (4.1)a	82.0 (4.2)b
GR	— —	91.0 (5.9)a	— —	87.0 (1.7)b
Nearctic				
ID	95.4 (6.6)bc	95.8 (5.6)a	91.4 (5.5)bc	99.8 (11.4)b
CA-S	111.0 (7.5)c	100.0 (11.4)a	95.4 (6.4)c	82.8 (6.8)b
CA-C	97.5 (9.4)bc	— —	85.9 (5.9)abc	— —
WA-W	98.3 (5.3)c	— —	80.3 (5.0)abc	— —
WA-Y	87.5 (5.4)a	— —	71.2 (3.0)a	— —
F values ^c				
Treatments	4.13**	1.56 NS	3.32**	5.44**
Blocks	3.27**	2.33 NS	0.76 NS	1.89 NS

^a Population codes are associated with specific populations in Table 1.

^b Means within columns followed by dissimilar letters are significantly different ($P = 0.05$) according to Duncan's multiple range test.

^c NS, Not significant.

** $P < 0.01$.

of the open field approach in host-specificity determination of insects for biological control of weeds.

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